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The Colonization of Violets and *Speyeria* Butterflies on the Ash-Pumice Fields Deposited by Cascadian Volcanoes

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Abstract. Violently explosive eruptions from the volcanoes of the Cascade Range have deposited extensive ash-pumice fields that constitute an extremely xeric habitat for most types of plants and animals. This study examines the colonization of this habitat by nymphalid butterflies of the genus *Speyeria* together with their larval foodplants of the genus *Viola* (Violaceae). Study areas include ash fields associated with Mt. Washington, the Three Sisters volcano system, Mt. Newberry, Mt. Mazama, Mt. McLoughlin, and Mt. Shasta in Oregon and California. Some species of *Speyeria* and *Viola* have proven to be vigorous colonizers of the ash-pumice habitat, while other species have been completely excluded from this habitat due to restrictive limitations in their physiology and ecological adaptations. Successful colonizing species have invaded the ash fields from several different directions: (1.) adjacent regions of the high Cascades, (2.) the arid lowlands east of the Cascade Range, and (3.) the Sierra Nevada and Siskiyou Mountains south and west of the Cascades. These organisms demonstrate how plants and associated insects may colonize and adapt to new habitats created by volcanic eruptions in the Cascade Range.

Introduction

The nymphalid butterflies of the genus *Speyeria* are intimate associates of the herbaceous plant genus *Viola* (Violaceae), since the larvae of *Speyeria* feed exclusively upon the leaves and flowers of *Viola*. Together these plants and animals are widely distributed throughout much of North America, and are among the most ecologically versatile of organisms in terms of the diversity of habitats that they occupy. These habitats range from dense forests to open prairies; permanently wet bogs to arid deserts. In addition, violets and *Speyeria* butterflies are usually very sensitive indicator organisms to human-caused disturbances of natural communities. Indeed, many populations of these organisms have become extinct or are threatened with extinction due to human disturbances such as agriculture and suburban development. A good example are the extinctions of *Viola hallii* Gray and *Speyeria callippe* Boisduval in the Willamette Valley grasslands of western Oregon about 50 years ago (unpublished data).

One of the most unusual habitats occupied by *Viola* and *Speyeria* are the extensive volcanic ash-pumice fields associated with the stratovolcanoes of the Cascade Range. These volcanoes extend from Mt. Garibaldi in southern British Columbia south to Mt. Lassen in northern California. Most of these volcanoes have experienced many violently explosive eruptions of the recent Mt. St. Helens type during their long histories. During such eruptions, vast quantities of finely divided silicaceous ash and pumice are ejected, so that adjacent areas downwind from the volcano are buried under deep layers of this material. The most extensive ash-pumice field was produced by the cataclysmic destruction of Mt. Mazama about 6600 years ago, and covers hundreds of square kilometers in central Oregon extending from Crater Lake in northern Klamath County to the Paulina-East Lakes in southern Deschutes County. Harris (1980) has prepared a general review of the history and geological characteristics of the Cascadian volcanoes.

As the ash-pumice fields are deposited during eruptions, most biological life forms are completely exterminated as a result of burial and suffocation. For example, David V. McCorkle (personal communication) is currently monitoring the recovery of *Speyeria* populations near Yakima, Washington, following the recent eruption of Mt. St. Helens in May, 1980. Prior to this eruption, large populations of *S. callippe* and *S. coronis* Behr were found in the eastern foothills of the Cascades west of Yakima. The Mt. St. Helens eruption was relatively mild compared to many past historical eruptions of other Cascadian volcanoes, and only 6-20 cm. of ash was deposited in the region near Yakima in 1980. Nevertheless, almost no *Speyeria* were observed in this region during 1981 except for a single specimen of *S. coronis*. In dramatic contrast, the ash-pumice fields examined in this paper were created by the deposition of several meters of volcanic material (up to 75 meters near Crater lake), which must have virtually sterilized these areas of all pre-existing *Viola* and *Speyeria* populations. This paper will examine the probable origins of *Viola* and *Speyeria* populations that were able to invade and re-colonize these newly created volcanic habitats, plus the ecological characteristics and adaptations of the organisms to such habitats.

These ash-pumice fields constitute an extremely xeric habitat for plants and animals, since this finely divided volcanic material fails to retain moisture. In areas where the depth of ash exceeds 30 cm., there is very little moisture available to herbaceous plants in the surface soil during the summer growing season, with the exception of the moist areas adjacent to creeks, lake shores, and boggy seepage areas. Most deep ash fields only support a forest of small, shrubby Lodgepole Pine (*Pinus contorta* Dougl.). The forest floor is mostly barren except for scattered Bitterbrush (*Purshia tridentata* Pursh) and small tufts of grasses. However, areas with only a shallow layer of surface ash and pumice will support a more substantial forest of Ponderosa Pine (*Pinus ponderosa* Dougl.) or White Fir (*Abies concolor* Lindl. & Gord.). At the higher elevations, melting snowbanks are an important source of moisture in the spring and early summer, and permit the growth of some herbaceous plants such as lupines (*Lupinus* sp.) and Yellow Prairie Violet (*Viola nuttallii* Pursh.).

Methods and Materials

During the present study, field investigations were conducted on the volcanic ash fields of the Cascades from Mt. Washington in Linn County, Oregon, to Mt. Shasta in Siskiyou County, California, during 1974, 1975, 1980, and 1981. Specific study areas included: (1.) ash fields near Big Lake just north of Mt. Washington in Linn County, (2.) ash fields east of the Three Sisters volcanoes in Deschutes County, (3.) the Mazama-Newberry ash fields extending from Crater Lake eastward to Yamsey Mountain in Klamath County and northward to the Paulina-East Lakes in southern Deschutes County, (4.) ash fields at the summit of the Cascades south of Mt. McLoughlin and Lake-of-the-Woods in southern Jackson and Klamath Counties, and (5.) ash fields around Mt. Shasta in Siskiyou County.

In each study area, the habitat, vegetation type, sun exposure, and the consistency of the ash-pumice soil were noted (Table 1.). Individual violet plants were measured and observed during the course of their growing season, and samples of the associated *Speyeria* species were collected. Measurements included leaf length, total diameter of plants, and butterfly forewing length. The butterflies were also examined with regard to variation in the coloration of the ventral hindwings. In addition to samples of butterflies collected during the present study, older samples collected between 1950 and 1970 were examined in the collections of Ernst J. Dornfeld of Corvallis, Oregon, Oregon State University, and the National Museum of Natural History in Washington, D. C.

Origin of the *Speyeria* Butterflies

In order to understand how the violets and butterflies have colonized the ash-pumice fields of the Cascade Range, it is necessary to examine the origin and ecology of these organisms in adjacent non-volcanic regions of Oregon and northern California that have not been exposed to significant volanic activity during the past 50,000 years. In a previous study, Hammond (1974) examined the ecology of *Speyeria* butterflies across North America, and a brief summary of this ecology for the Pacific Northwest *Speyeria* is useful for the present study (see Table 2).

Eight different species of *Speyeria* are widely sympatric in the mountains through much of the Pacific Northwest from western Montana and Wyoming to the Cascade Range and southward through the Sierra Nevada of California. Although adult butterflies frequently fly together, there is

Table 1. Populations of *Viola* and *Speyeria* that have colonized the volcanic ash-pumice fields of the southern Cascade Range.

Volcanoes	Habitat	Viola	Speyeria
Mt. Shasta	Red Fir forest	*purpurea*	*egleis*
Mt. McLoughlin	high elevation Lodgepole Pine forest	*purpurea, nuttallii*	*atlantis*
	lower elevation mixed conifer forest	*purpurea, nuttallii*	*egleis*
Mt. Mazama, Mt. Newberry, Three Sisters	Lodgepole Pine forest	*purpurea*	*egleis, zerene*
	moist, open areas	*purpurea, nuttallii*	*callippe, coronis*
	wet, boggy meadows	*palustris, adunca*	*mormonia*
Mt. Washington	mixed conifer forest	*nuttallii, orbiculata*	*atlantis, hydaspe*

Table 2. Typical habitats of *Viola* and *Speyeria* species in non-volcanic regions of the Pacific Northwest.

Habitat	Viola	Speyeria
exposed wet meadows	*palustris, adunca*	*mormonia*
sheltered wet meadows with thickets of willows, alders, etc.	*glabella, palustris, adunca*	*cybele*
dry meadows and grassy prairies at high elevations	*nuttallii*	*atlantis*
dense, moist spruce-fir and pine forests	*glabella, orbiculata, adunca, nuttallii*	*hydaspe*
open, dry pine forests	*adunca, nuttallii, purpurea*	*zerene*
exposed, dry rocky ridges and talus slopes at high elevations	*purpurea*	*egleis*
sagebrush-juniper communities	*nuttallii, purpurea, douglasii, beckwithii*	*callippe, coronis*

usually fairly sharp segregation among species in the types of habitat utilized by the larvae. Each species appears to be adapted for utilizing a particular type of habitat, although *Speyeria* larvae are not adapted to any particular species of violet and will feed upon any violet that happens to be growing in the appropriate habitat (Hammond, 1974). At the same time, most *Speyeria* species exhibit considerable ecological plasticity, and frequently invade the habitats of related species when the latter are absent for one reason or another (see contrasts between West Coast and Rocky Mountain *S. mormonia, S. atlantis,* and *S. hydaspe* cited below). These observations of such "ecological release" provide indirect evidence that the ecological segregation of *Speyeria* species is largely the result of interspecific competition for the larval foodplant in the various habitats.

Two species, *S. mormonia* Boisduval and *S. cybele leto* Behr, occupy wet, boggy meadow habitats. *Speyeria mormonia* favors completely open, exposed meadows that are free of shrubs and small trees, while *S. cybele leto* favors more sheltered meadows with thickets of willows (*Salix* sp.) and small trees. Another species, *S. atlantis dodgei* Gunder, also occupies open meadows at the higher elevations in the mountains, but only dry, well-drained meadows in contrast to the boggy meadows occupied by *S. mormonia*. It should be noted that these relationships change in the Rocky Mountains, where *S. mormonia* occupies both the dry and wet meadow habitats, while Rocky Mountain subspecies of *S. atlantis* occupy spruce-fir and aspen forest habitats.

However, the primary forest species in the Pacific Northwest is *S. hydaspe* Boisduval, which occupies spruce-fir forests at high elevations and dense, moist Ponderosa Pine forests at middle elevations. *Speyeria zerene* Boisduval is adapted to more xeric conditions and replaces *S. hydaspe* in very dry, open pine forests. The species also extends out into the highly xeric sagebrush-juniper habitat to some extent as well. *Speyeria callippe* Boisduval is adapted to the most extreme of xeric habitats, and occupies sagebrush-juniper communities throughout much of western North America at the lower elevations. West of the Cascade and Sierra Nevada Ranges, *S. callippe* occupies dry, open grassland and oak-pine shrubland at low elevations. At high elevations in the mountains, *S. callippe* is often replaced in the xeric habitat by *S. egleis* Behr, which usually occupies barren, exposed rocky ridgetops and talus slopes within the spruce-fir zone. The last species, *S. coronis* Behr, is another semidesert species like *S. callippe*, and usually occupies sagebrush-juniper habitats or open, dry pine forests. However, *S. coronis* is a much larger species than the others, and appears to require a much larger biomass of the larval foodplant (based partly upon observations of reared larvae). Thus, *S. coronis* is commonly associated with moist areas near creeks, lakes, and seepage areas in these arid regions where the violets produce a more vigorous growth.

Origin of the Violets

Seven different species of violets provide important larval foodplants for *Speyeria* butterflies in the Cascade Range (Table 2). *Viola palustris* L. occupies wet, boggy meadows near creeks, lakes, and seepage areas throughout much of western North America, but only meadows with a permanent source of water. In contrast, *V. adunca* J. E. Smith var. *bellidifolia* Greene occupies wet, boggy meadows that dry out during July and August. Both of these violets are very common in wet meadows at high elevations throughout the Oregon Cascades, and are the primary larval foodplants of *S. mormonia* and *S. cybele leto*. A third violet, *V. nuttallii* Pursh. var. *linguaefolia* Nutt., occupies dry, well-drained meadows and open grassy prairies at high elevations throughout much of western North America, and is the primary larval foodplant of *S. atlantis dodgei* in the Cascade Range.

Two species of mesic forest violets, *V. glabella* Nutt. and *V. orbiculata* Geyer, occupy the moist spruce-fir forests at high elevations and are the primary foodplants of *S. hydaspe* in the Cascade Range. At lower elevations, the drier Ponderosa Pine forests are occupied by *V. nuttallii*, *V. purpurea* Kell., and the typical form of *V. adunca* J. E. Smith. These violets are utilized by the larvae of both *S. hydaspe* and *S. zerene*. Both *V. nuttallii* and *V. purpurea* also extend into the sagebrush-juniper zone where they are utilized by *S. callippe* and *S. coronis*. In addition, the xerophytic *V. purpurea* var. *venosa* S. Wats. occupies exposed, rocky ridgetop and mountainsides at high elevations throughout much of western North America, and is the primary larval foodplant of *S. egleis*.

However, the most extreme xerophytes among the North American violets belong to the *V. douglasii-beckwithii* species complex. *Viola douglasii* Steudel occupies dry, open grasslands and oak-pine brushland at low elevations in California, extending from northern Baja California north to Medford and Klamath Falls, Oregon. There is also an isolated relict population of *V. douglasii* along the Metolius River in Jefferson County, Oregon. East of the Sierra Nevada and Cascade Ranges, *V. douglasii* is replaced by the closely related *V. beckwithii* Torr. & Gray in the sagebrush-juniper community. Both violets are primary larval foodplants for *S. callippe* and *S. coronis*.

Colonization of Mt. Shasta Ash Fields

According to Harris (1980), Mt. Shasta represents one of the largest stratovolcanoes in the world, reaching 4317 meters in elevation. The volcano actually consists of a series of eruptive cones that have been built upon each other. The most recent major cone, Shastina, has only developed during the past 10,000 years and now reaches 3759 meters in elevation. Violently explosive eruptions of massive proportions apparently took place during this period, and pyroclastic flows covered much of the territory near the base of the volcano. Today the steep upper slopes of Mt. Shasta are covered with glaciers and snow during much of the year. The lower slopes of the mountain are covered with a thick layer of finely divided volcanic ash and pumice that supports a well developed forest of Shasta Red Fir (*Abies magnifica* A. Murr. var. *shastensis* Lemmon). A particularly deep ash-pumice field extends to the northeast of Mt. Shasta and only supports a sparse forest of Lodgepole Pine.

The primary violet and *Speyeria* butterfly found on the Mt. Shasta ash fields are *V. purpurea* and *S. egleis* respectively. Both species are very common in the Red Fir forests at the higher elevations on the volcano. The violets grow in the loose ash soil of the forest floor, and even form a thick carpet of plants in some areas of the forest. Adult butterflies fly mostly in sunny glades and clearings within the forest near the violets, and only occasionally stray out into the more open, non-forested areas of the mountain.

This last point is important when considering the origins of *S. egleis* in the non-volcanic habitats of the Sierra Nevada, Warner, and Salmon-Siskiyou Mountains. In these mountains, *V. purpurea* is very common in both dry, open Ponderosa Pine forests and on barren, rocky ridgetops and exposed mountainsides. *Speyeria zerene* usually occupies the pine forest habitat while *S. egleis* occupies the open, rocky habitat throughout these mountains. Likewise, *S. zerene* is the dominant species in the open, dry pine forests surrounding Mt. Shasta at the lower elevations. However, the occupation by *S. egleis* of the Red Fir forests at higher elevations on Mt. Shasta clearly represents a marked ecological shift from the open, rocky habitat of *S. egleis* in the Sierra Nevada, Warner, and Salmon-Siskiyou Mountains. The reasons for this sharp ecological shift may have the following possible explanation.

Speyeria zerene exhibits a definite preference for relatively warm forests at lower elevations, while *S. hydaspe* usually occupies cool, moist spruce-fir forests at higher elevations. The failure of *S. hydaspe* to occupy the Red Fir forests on Mt. Shasta may be due to the extremely xeric nature of the loose ash-pumice soil found on most of Mt. Shasta. *Speyeria hydaspe* does occur in limited numbers in small stands of particularly dense, moist forest on the lower slopes of Mt. Shasta, so the species does have the opportunity to invade the upper Red Fir forests. Therefore, it would appear that the failure of *S. hydaspe* to successfully occupy this forest habitat has allowed *S. egleis* to make the ecological shift into the forest habitat as an opportunistic colonizer. The major part of this colonization probably took place during the past few thousand years following the completion of Mt. Shasta's massive explosive eruptions from the recently built Shastina cone. These *S. egleis* populations also extend eastward from Mt. Shasta into the Medicine Lake volcano system.

Colonization of Ash Fields Near Mt. McLoughlin

Extensive ash-pumice fields are also found along the summit of the Cascade Range south of Mt. McLoughlin in southern Jackson County, Oregon, and south of Lake-of-the-Woods in southern Klamath County. These ash fields support either pure forests of Lodgepole Pine or mixed forests of Lodgepole Pine, Ponderosa Pine, and White Fir (*Abies concolor*). *Viola purpurea* is still common in this area, but is not so abundant as on Mt. Shasta. Instead, the dominant violet on these ash-pumice fields is *V. nuttalli* var. *linguaefolia*, a species that occupies dry open meadows and grassy prairies at high elevations throughout the Cascade Range. In the ash fields near Mt. McLoughlin, both *V. purpurea* and *V. nuttallii* often form a dense carpet of plants in the ash soil of open clearings within the pine forest, but the individual plants are usually very small rosettes measuring only 2-6 cm. in diameter.

The primary *Speyeria* that utilizes *V. nuttallii* in the high mountain meadows and prairies of the Cascade Range is *S. atlantis dodgei*, and this species has followed *V. nuttallii* into the ash-pumice fields south of Mt. McLoughlin. *Speyeria atlantis* is the dominant species on the ash fields along the summit of the Cascades in Jackson County, although a few *S. egleis* are also present in this area. However, there is a rapid shift in dominance over to *S. egleis* on the ash fields south of Lake-of-the-Woods in Klamath County.The reasons for these replacements between *S. egleis* and *S. atlantis* are not really known, but are thought to be the result of subtle differences in temperature and moisture in the two areas. For example, the ash fields along the summit of the Cascades are usually covered with a deep snowpack during the winter, while the lower elevations along the eastern slope of the Cascades in Klamath County usually receive much less snowfall.

A very similar situation exists in the central Oregon Cascades. Both *V. purpurea* and *S. egleis* are absent from the summit of the Cascades in the Mt. Washington ash fields of Linn County, but both species are present on the eastern slope near the Metolius River and east of the Three Sisters volcanoes in Jefferson and Deschutes Counties. The ash fields north of Mt. Washington near Big Lake support large populations of *V. nuttallii* just as in the Mt. McLoughlin area, and some *S. atlantis dodgei* are also associated with these violet populations. However, both *V. orbiculata* and *S. hydaspe* have also penetrated into the Lodgepole Pine forests around Mt. Washington from the adjacent spruce-fir forests on Santiam Pass. This is the only instance where a mesic species of violet and *Speyeria* butterfly have been observed to occupy a xeric ash-pumice habitat, and is probably due to the moisture received from the heavy snowpack that accumulates during the winter along the Cascade summit.

Colonization of the Mt. Mazama-Mt. Newberry Ash Fields

The deepest and most extensive ash-pumice fields in the Oregon

Cascade Range were deposited by massive, violently explosive eruptions from Mt. Mazama and Mt. Newberry in northern Klamath County and southern Deschutes County. These ash fields also extend northward in Deschutes County along the eastern slope of the Three Sisters volcanic system; a complex of numerous volcanoes that have also produced significant eruptions of ash and pumice. The most important eruption was the cataclysmic explosion that destroyed Mt. Mazama about 6600 years ago, creating the modern Crater Lake caldera. Likewise, Mt. Newberry has also been replaced with a deep caldera crater that is occupied by Paulina Lake and East Lake today. The deepest ash fields extend from the south end of Crater Lake National Park eastward to Yamsey Mountain in Klamath County and northward to the Paulina-East Lakes in Deschutes County, an area covering more than 3500 square kilometers. According to Harris (1980), the depth of these ash-pumice fields ranges from 7-15 meters, and reaches a depth of 75 meters in some of the creek valleys near Crater Lake. Before this cataclysmic eruption, Mt. Mazama was one of the largest Cascadian stratovolcanoes, reaching an estimated height of 3660 meters. Afterwards, an estimated 65 cubic kilometers of volcanic material were expelled from the mountain to produce these ash-pumice fields. The Newberry caldera is thought to have been created through a series of violently explosive eruptions according to Harris, rather than in a single cataclysmic eruption as with Mt. Mazama. The most recent eruptions are thought to have taken place less than 1000 years ago. As Harris has pointed out, Mt. Newberry is a huge shield volcano extending 32 kilometers in diameter with some 200 parasitic cinder cones on the slopes of the volcano. In addition to explosive eruptions of ash and pumice, the volcano has also produced numerous thicker flows of basalt and obsidian during the course of its long history.

The ash fields from Crater Lake to the Paulina-East Lakes are extremely dry, and only support a sparse, scrubby forest of Lodgepole Pine in most areas, although Ponderosa Pine is found in some areas where the ash soil is shallower. As a result, the forest floor is mostly barren and devoid of vegetation except for scattered shrubs of Bitterbrush (*Purshia tridentata*) and small tufts of grasses. However, there are many places in these ash fields where ground water does come to the surface, producing small creeks, seepage areas, and wet, boggy meadows. Stands of willows (*Salix* sp.) and Quaking Aspen (*Populus tremuloides* Michx.) occupy these wet areas together with a large diversity of herbaceous plants including wild strawberry (*Fragaria* sp.), columbine (*Aquilegia formosa* Fisch.), delphinium (*Delphinium menziesii* D.C.), penstemons (*Penstemon* sp.), Indian paintbrush (*Castilleja* sp.), and various composites.

Of the three species of xerophytic violets found along the eastern slope of the Oregon Cascades, only *V. nuttallii* var. *linguaefolia* and *V. purpurea* have been able to colonize the Mazama ash fields. *Viola douglasii* is found on the juniper-sagebrush hillsides around Klamath Falls in southern Klamath County and again along the Metolius River in Jefferson County. The region between these two widely disjunct populations was buried under the Mt. Mazama ash fall, and the violet has never been able to successfully recolonize the Mazama ash fields. The thick rootstalk of *V. douglasii* appears to be adapted to a firm rocky or hard clay substrate, and it does not grow well in a loose, finely divided ash-pumice soil.

Although *V. nuttallii* grows well in the ash-pumice soil, it apparently requires considerable moisture in the spring, and is mostly restricted to the higher elevations where there is a heavy snowpack in the winter, for example around the Paulina-East Lakes. Only *V. purpurea* is common and widely distributed in the pine forests of the Mazama ash field, and it is largely restricted to the moist zones of pine forest near the edges of creeks and boggy seepage areas. Even in this fairly moist habitat, the individual plants of *V. purpurea* are very small, measuring only 2-5 cm. in diameter.

Two species of mesophytic violets have been able to colonize the wet areas in the Mazama ash fields from the high mountains to the west. *Viola palustris* is strongly restricted to the edges of creeks and lakes that remain permanently wet through the year, while *V. adunca* var. *bellidifolia* is extremely abundant in wet, boggy meadows that dry out for part of the summer. The violets often form a dense carpet of plants in many parts of these meadows, but the individual plants are very small as in *V. purpurea*, measuring only 1-5 cm. in diameter.

Five different species of *Speyeria* have been able to colonize the Mazama ash fields, including *S. mormonia, S. egleis, S. zerene, S. coronis,* and *S. callippe*. Moeck (1957) and Tilden (1963) previously studied the *Speyeria* populations in this region. *Speyeria mormonia* occupies the wet, boggy meadows, utilizing *V. palustris* and *V. adunca* as larval foodplants. The butterfly has almost certainly invaded and colonized the Mazama ash fields together with these violets from the adjacent high Cascades to the west. However, *S. callippe* and *S. coronis* occupy dry, open habitats, and have probably invaded the Mazama ash fields from the adjacent sagebrush-juniper lowlands to the east, which constitute the usual habitat of these xeric species. Because the Mazama ash fields are mostly covered with Lodgepole Pine forests, *S. callippe* and *S. coronis* are usually rather rare in this region due to the scarcity of open habitats, but particularly large populations breed in the open, moist areas around the Paulina-East Lakes. *Speyeria callippe* is the dominant species around these lakes, while *S. coronis* is less common and *S. mormonia* is restricted to the wet, boggy habitats. Thus, mesic *S. mormonia* and xeric *S. callippe* appear to have invaded and colonized the Mazama ash fields from opposite directions.

Speyeria zerene and *S. egleis* are the dominant species in the Lodgepole Pine forests of this region, but they are mostly restricted to the moist zones of pine forest near the creeks and boggy seepage areas like their *V.*

purpurea foodplant. While *S. zerene* is the usual *Speyeria* to occupy dry, open pine forests throughout western North America, it is often rather scarce on the Mazama ash fields, and is often replaced in this habitat by large populations of *S. egleis*. This latter species has invaded and colonized the Mazama ash fields from the Mt. McLoughlin and Lake-of-the-Woods ash fields in southern Klamath County. Evidence of this invasion is suggested by the physical characteristics of butterflies from clinal populations between Lake-of-the-Woods and Crater Lake. In addition to occupying pine forests at low elevations east of Crater Lake, *S. egleis* also occupies barren pumice fields around the rim of Crater Lake itself.

The unique feature of these Mazama *S. egleis* is their very small size, which appears to represent an adaptation to the small, dwarfed size of their larval foodplant. For comparison, a sample of 64 *S. egleis* males from near Lake-of-the-Woods had a forewing length range of 23-28 mm. ($\bar{X} = 26$ mm.), while a sample of 71 males collected on the Mazama ash fields east of Crater Lake had a range of 21-25 mm. ($\bar{X} = 23$ mm.). As such, the Mazama *S. egleis* rank among the smallest of all *Speyeria* butterflies in existence. These samples are illustrated in Figure 1., and the difference between the sample means is highly significant ($\chi^2 p<0.0001$). Moreover,

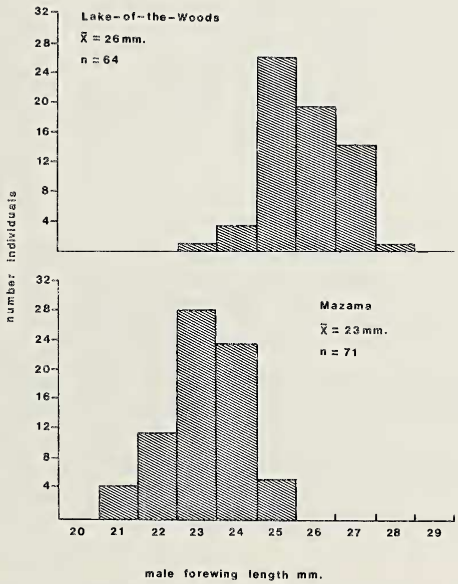

Fig. 1. Comparison of male forewing length in *Speyeria egleis* samples from the Mazama ash fields of northern Klamath Co., Oregon, and near Lake-of-the-Woods in southern Klamath Co.

laboratory rearing experiments conducted by D. V. McCorkle of Monmouth, Oregon, and O. D. Spencer of Lincoln, Nebraska, have shown that this dwarfed size is under strong genetic control, and is not merely an environmentally induced phenotype. McCorkle reared samples of *S. egleis* from several different areas under approximately identical conditions, and the largest specimens from the Mazama region of Klamath County reached 25 mm. while the largest from the Siskiyou Mountains of Josephine County reached 27 mm. Thus, the size of reared specimens from different areas closely corresponds to the size range of wild specimens, suggesting a strong genetic component to the determination of forewing length.

This Mazama form of *S. egleis* also differs from the Mt. Shasta-Mt. McLoughlin populations in coloration, exhibiting relatively little dark basal suffusion on the dorsal wing surfaces and often a reddish brown ventral hindwing. In contrast, the Mt. Shasta-Mt. McLoughlin *S. egleis* usually exhibit more extensive dark basal suffusion on the dorsal wing surfaces and a black-brown or umber brown ventral hindwing.

The Mazama form of *S. egleis* has a wide distribution in the central Oregon Cascades that corresponds very closely with the distribution of the ash-pumice fields in this region, extending from Crater Lake eastward to Yamsey Mountain and northward to the Paulina-East Lakes and the Three Sisters volcanoes in Deschutes County. Since this habitat did not even exist until after the destruction of Mt. Mazama about 6600 years ago, it would appear that this distinctive Mt. Mazama form of *S. egleis* has only evolved from the Mt. Shasta form during the past 6000 years or so. Considering the fact that the Mazama ash fields represent a particularly harsh, xerophytic environment, it is interesting to observe that this organism has been able to colonize and evolve in this new environment in such a short time period.

While *S. egleis* has successfully colonized the Mazama ash fields, *S. cybele leto* has been completely excluded from this region, and displays the same relict, disjunct distribution as *Viola douglasii*. Colonies of *S. cybele* are found around Klamath Lake in southern Klamath County and again along the Metolius River in Jefferson County, but the species has not been able to recolonize the intervening Mazama ash fields. *Speyeria cybele leto* is a large butterfly and apparently requires a large biomass of the larval foodplant, but the violets that grow in volcanic ash habitats are usually too small to support such a large butterfly (based partly upon observations of larvae reared by D. V. McCorkle).

Conclusions

The colonization of volcanic ash-pumice fields in the southern Cascade Range by violets and *Speyeria* butterflies is summarized in Table 1. For comparison, the normal habitats of the plants and animals in non-volcanic areas are summarized in Table 2. These organisms demonstrate how plants and associated insects may colonize and adapt to new environments recently created by the eruptions of Cascade volcanoes. It is interesting that some violet species such as *V. purpurea* and *V. nuttallii* have been vigorous colonizers of the ash-pumice fields, while other violets such as *V. douglasii* have been conspicuously unsuccessful. *Speyeria egleis* has followed *V. purpurea* into the ash fields of Mt. Shasta, Mt. McLoughlin, and Mt. Mazama from the exposed, rocky habitats of the Sierra Nevada, Siskiyou, and Warner Mountains. In contrast, *S. atlantis dodgei* has followed *V. nuttallii* into the Mt. McLoughlin ash fields from the dry, open meadows and prairies of the high Cascades. Likewise, *S. mormonia* has followed *V. palustris* and *V. adunca* into the Mt. Mazama ash fields from the wet, boggy meadows of the high Cascades. However, both *S. callippe* and *S. coronis* have invaded the Mt. Mazama ash fields from the sagebrush-juniper lowlands east of the Cascade Range. *Speyeria zerene* is also a typical resident of the Mt. Shasta, Mt. McLoughlin, and Mt. Mazama regions where it occupies open dry pine forests; the same habitat the species occupies throughout much of western North America. However, *S. cybele leto* has been effectively excluded from ash-pumice habitats due to its requirement for a large biomass of the larval foodplant.

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